remarked its narrower and more slender leaves, but referred it to *L. occidentalis* Coult. & Rose because of the agreement in fruit structure between the California plant and those from further north.

The most critical distinguishing feature between the coastal and delta plants is that the leaves of the latter are not only narrower, more slender, and usually shorter, but that they are truly terete, have proportionately fewer septae, particularly toward the apex, and that these septae are so obscure that they are likely to remain unobserved. The fruit characters, upon which Hill relied so heavily to distinguish species, are essentially identical. Even chromosome number is of no taxonomic assistance since *L. masonii* like *L. occidentalis,* has a complement of $n = 22$; both are presumably tetraploid. The taxon referred to as *Lilaeopsis sp.* in Constance, Chuang & Bell (1976, No. 481, p. 619) is *L. masonii.*

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VEGETATION ANALYSIS OF A NORTHERN CALIFORNIA COASTAL PRAIRIE: SEA RANCH, SONOMA COUNTY, CALIFORNIA

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The northern coastal prairies of California are distributed along parts of the coastal zone from the California-Oregon border south to Monterey Bay. Previous authors have outlined the natural history and the distribution of species of the coastal grassland ecosystem (Beetle, 1947; Burcham, 1957; Munz, 1973; Crampton, 1974; Ornduff, 1974) and a number of floristic surveys have been completed (Davy, 1902; Peñalosa, 1963; Barbour, 1970, 1972; Howell, 1970; Hardham and True, 1972). Ecological analysis of the coastal grassland, however, has been limited (Huffaker and Kennett, 1959; Batzli and Pitelka, 1970; Barbour et al., 1973; Elliott and Wehausen, 1974; Davidson, 1975); Heady et al. (1977) also reached this conclusion.

In 1974, we began an analysis of the coastal perennial grassland community at Sea Ranch, Sonoma County, California. The two major goals of this program are first to document the structure of a coastal grassland that has not been grazed by livestock for approximately 10 years, and secondly to develop hypotheses about dominance and diversity relationships suitable for experimental tests.

For many years the coastal grasslands have been strongly influenced by persistent livestock grazing. With increased coastal development for residential purposes and with the proliferation of park reserves large sections of the coastal grassland are no longer grazed and are undergoing changes in species composition and standing crop. We set out to document the changes as one such area recovers from grazing. Over the long term we hope to understand the regulation of dominance, species diversity, and patchiness of vegetation distribution by studying population parameters of selected species using methods described elsewhere (Foin and Jain, 1976).

This paper presents the results of our first survey of the Sea Ranch grasslands in 1974. An annotated species list for the Sea Ranch costal terraces is being published elsewhere (Hektner and Foin, 1977).

The Study Site

Sea Ranch (38° 40′ N, 123° 24′ W) is a low density subdivision approximately 180 km north of San Francisco (Fig. 1). It is situated along 16 km of the northern Sonoma County coastline and extends up to 2 km inland. The 729 ha of terrace grassland under study are bounded by California State Highway 1 on the east, Gualala Point Sonoma County Park on the north, the Sea Ranch southern boundary line, and the Pacific Ocean. Approximately 95% of the coastal terrace area has been reserved as permanent open space by the Sea Ranch Homeowner's Association and allowed to develop with minimum disturbance. Hence, these open areas permit long term studies of the dynamics of the coastal prairie.

The area that is now Sea Ranch was included in an 8,100 ha Spanish land grant, known as Rancho German, given to Ernst Rufus in 1846. Lumbering soon became an important industry and a mill was established at the mouth of the Gualala River. The grant was eventually broken up and one of the parcels sold was Black Point (now part of the Sea Ranch), from which lumber and cattle were shipped to San Francisco (Morgan and Morgan, 1974). Horses, cattle and sheep grazed the Sea Ranch area (then known as Del Mar Ranch) continuously until the mid-1960's. Parts of the terrace were occasionally plowed for planting peas, potatoes, and even artichokes. Unspecified species of clover were also sown by the former owner to provide additional forage for sheep (Ohlson, pers. comm.). Development began in 1963 in the southern portion, and pastures were abandoned as it proceeded northward. The last sheep were removed from the northern section in 1968, but cattle grazed the north end from 1967 to 1969.

Like most of northern California, Sea Ranch receives most of its precipitation during late fall, winter, and spring. Records kept by local residents on the terrace (elevation 22 m) and published in the *Independent Coast Observer* (a local newspaper) show a 5-year average seasonal

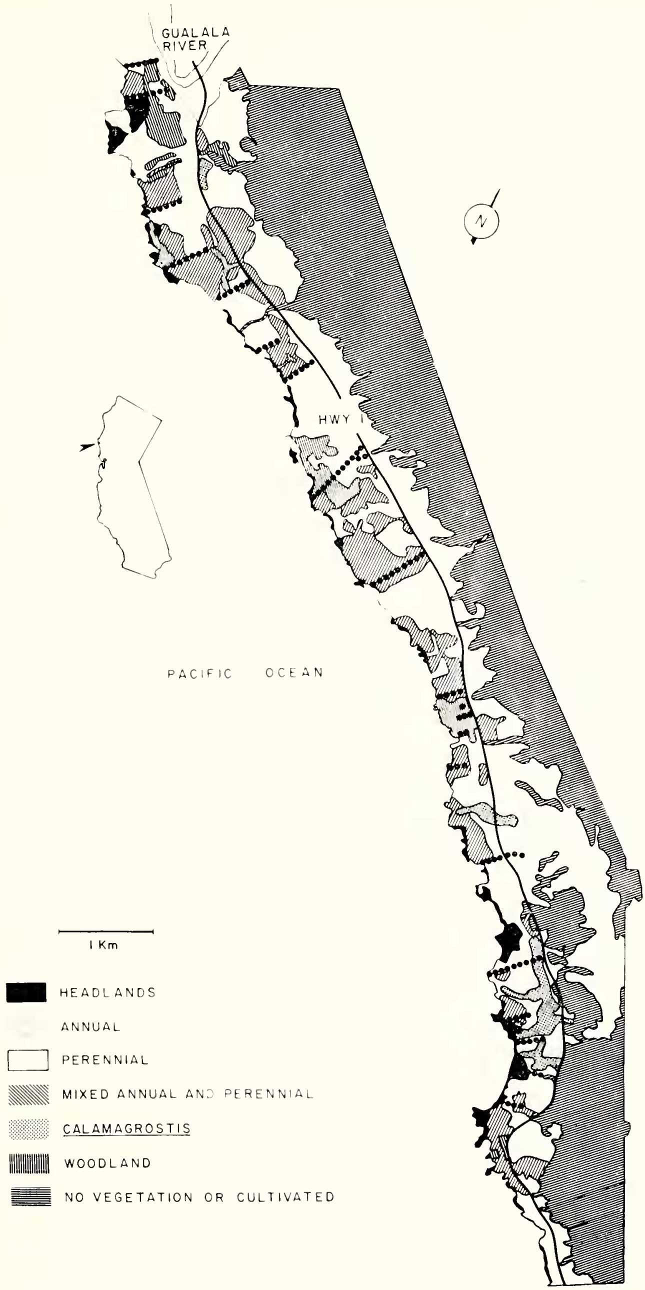

FIG. 1. Distribution of major vegetation types at Sea Ranch, California. Rows of dots represent hedgerows of *Cupressus macrocarpa*.

rainfall of 842 mm (range, 458–1308 mm), with 92% falling from October through March. For the same period (July 1970–June 1975), at the top of German Ridge (elevation 274 m) 6.4 km to the north, seasonal rainfall averaged 1609 mm (range, 932–2475 mm).

Fog associated with periods of slack winds during summer contributes an unknown amount of moisture. Wind direction varies seasonally, coming mainly from the north and northwest during summer, and from the south and southeast during winter. Checks of wind velocities during planning studies for the development of Sea Ranch (Lawrence Halprin and Associates, unpubl.) during 1954 through 1961 showed that in general winds of less than 5 kph seldom occurred more than 10% of the time in any month. Winds in the 6–24 kph class persisted for 50–65% of every month and 25–30% of any month had winds in excess of 26 kph.

There are no continuous temperature records for Sea Ranch, but mean monthly temperature records are available for the past 43 years for Fort Ross, 31 km south. Annual mean temperature is above 11C, with monthly means ranging from 6.5C in the winter to 15C in the summer (Davidson, 1975).

Due to the proximity of Fort Ross to Sea Ranch, the long-term climatic records for Fort Ross were used to construct a Thornthwaite climatic diagram (Fig. 2) as an approximation of the Sea Ranch climate. Climatic data representing 86 years of recorded precipitation and 11 years of temperature (U.S. Environmental Data Service, 1964) were used to determine potential evapotranspiration and thus calculate the water balance throughout the year. We used an unpublished computer program written by Randall and Major of the U.C. Davis Botany Department and calculations follow Black (1966) and Thornthwaite et al. (1957). These calculations assume 100 mm of water available from soil storage and that the rate of water removal by plants from the soil is proportional to the amount remaining in the soil.

As in most areas having Mediterranean climates, growth is slow during winter, peaks in spring and fall and declines sharply during summer.

Most of the terrace area on the coastal side of Highway 1 is nearly level with slopes of less than 10%. The coastal terrace consists of two wave-cut benches, both formed during the Quaternary, but subsistence and erosion have greatly obliterated their boundaries (Moore, pers. comm.).

Soils of the terrace areas are predominantly of two types: Baywood loamy sand and Rohnerville loam (U.S.D.A., 1972). The Baywood series, generally directly adjacent to the ocean, consists of very well drained loamy sand formed in wind-modified sandy coastal plain sediments and soft sandstone. The Rohnerville soils, formed in material weathered from soft sandstone, are moderately well drained, with a subsoil mainly of sandy clay. At one point where the terrace is very narrow a small area of Kneeland loam extends down to the ocean bluff at 15–30% slopes. Be-

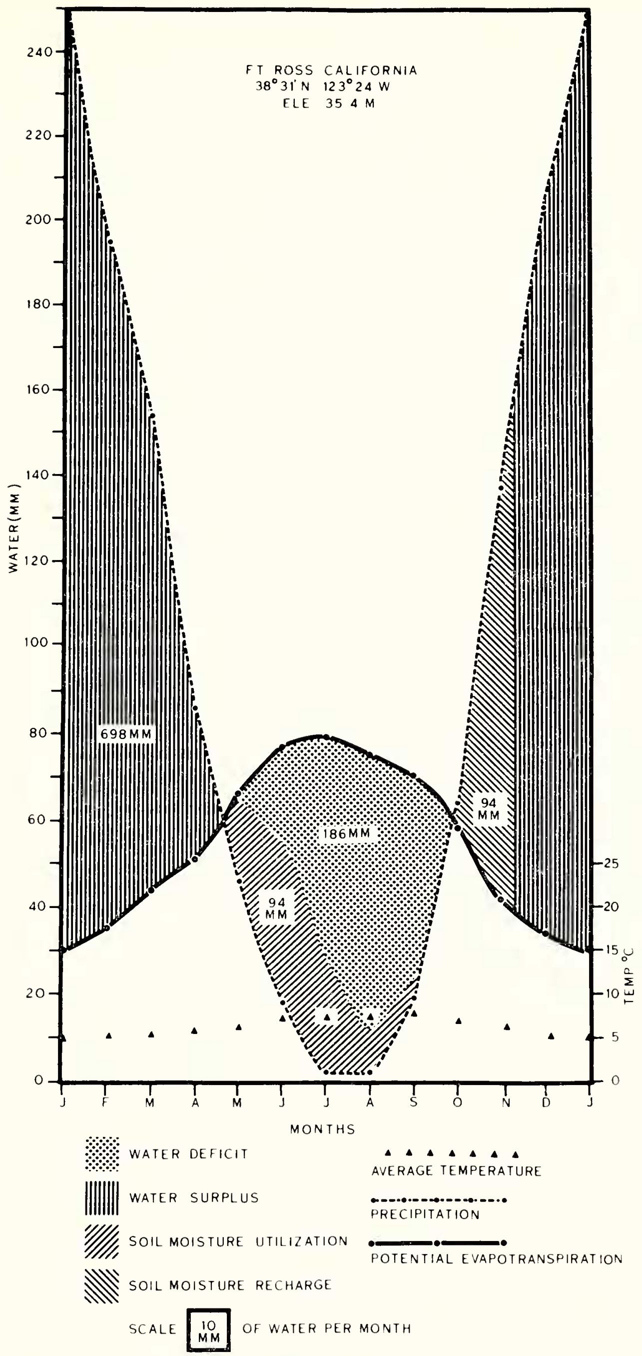

FIG. 2. Thornthwaite climatic diagram for Fort Ross, California.

cause of their thick dark color, granular structure, and generally high base saturation, these soils are considered typical prairie soils similar to those of the Midwest (Ornduff, 1974; Burcham, 1957; Barshad, 1946). In addition there are two small areas of dune sand, both stabilized by beachgrass *(Ammophila arenaria)*.

Methods and Materials

The first step in the vegetation analysis was the production of a map to establish the location of major vegetation types and to estimate the contribution of each type to vegetative cover (Fig. 1). This map was constructed from infrared aerial photographs taken by the National Aeronautics and Space Administration for the U.S. Army Corps of Engineers using an RC-86″ focal length camera at an altitude of 6,096 m in 1972, and at 914 m in 1974. Slide projections were superimposed on a base map and differences in infrared color were used to establish tentative vegetation boundaries. Boundaries were later verified by ground survey.

Vegetation units selected for sampling included headlands, shrub (lupine)-dominated, mixed grassland, perennial grassland, and *Calamagrostis*-dominated. The criteria used to distinguish each unit were as follows: headlands–areas along the ocean bluffs with very low vegetative height, usually 20 cm or less, with abundant forbs; lupine areas–where lupine cover *(Lupinus arboreus)* extended through more than 2–3 contiguous adult individuals (the patch of bushes defined the area); grasslands–mixed, when neither annual nor perennial grass relative cover exceeded 50%, and perennial, those having $\geq$ 50% relative cover of perennial grass species; *Calamagrostis* areas–where those in which the relative cover of *Calamagrostis nutkaensis* was $\geq$ 50%. These five types were selected because they were quantitatively important (as determined from the aerial map) or were an essential element in the successional sequence, or both. In particular, annual grasslands were not sampled because they were quantitatively unimportant and because they appear to be restricted to sites where disturbance from construction or horse grazing continues to be heavy.

Sampling of the vegetation was conducted during August and September, 1974, at 5 sites ranging from 4,500–16,000 m^2. At each site, sample quadrats were placed randomly within a 10 m distance along parallel transects themselves placed randomly within a 10 m band, giving one sample per 100 m^2. For each quadrat percentage bare ground and cover of each species in the quadrat were recorded. Each species was coded for analysis using mnemonics in Reed et al. (1963) and tabulated using cross tabulation and Chi^2 homogeniety tests from the SPSS/FASTABS program (Nie et al., 1975). Taxonomy and nomenclature follow Munz (1973) except for *Deschampsia holciformis,* which follows Crampton (1974). Voucher specimens have been deposited in the Botany Department Herbarium of the University of California, Davis.

Quadrat size varied, depending on the mean diameter of the species. *Lupinus arboreus* and *Calamagrostis nutkaensis* were sampled in quadrats of 50.25 m^2 area; bunchgrass, 12.26 m^2; and all others, 0.25 m^2. Circular quadrats were used with the differing sized quadrats placed concentrically for sampling of all species.

Cover esimates were made using a Domin Index (modified by Major, after Evans and Dahl, 1955). In this study, the scale was defined as follows: 1 = 1 or 2 individuals, cover less than 0.01%; 2 = few individuals, cover less than 0.1%; 3 = several individuals, cover less than 1%; 4 = numerous individuals, cover less than 4%; 5 = cover 5–10% of the total area; 6 = cover 11–20% of the total area; 7 = cover 21–33% of the total area; 8 = cover 34–50% of the total area; 9 = cover 51–75% of the total area; 10 = cover 76–90% of the total area; and 11 = cover 91–100% of the total area.

Note that values 1–3 are measures of density; those from 4–11 are true cover estimates. Total cover for a species was estimated as the percentage of the quadrat occupied by a vertical projection onto the ground surface of all individuals of that species. The Domin Index was also used to estimate bare ground. For tabulation purposes, Domin indices were converted to the midpoint value of their corresponding percentage range; for example, a Domin value of 11 = 91–100% is equivalent to 95.5%.

Results

As might be expected, analysis of the vegetation map (Fig. 1) reveals that major map units (headlands, perennial grasslands (including *Calamagrostis* areas), mixed grasslands, annual grasslands, and woodland) are not uniformly distributed along the coastline-inland gradient. To show this, 61 transect lines perpendicular to the coast were randomly placed on the map and 30 chosen randomly for sampling of vegetation type at each of 6 stations 0, 30, 122, 244, 488, and 975 m from the bluff edge. Chi^2 tests for uniform distribution of each type along the inland gradient revealed that 3 types (perennial grasses, headlands, and woodlands) are significantly localized $p < 0.025$) with the modal frequency from coastline inland in the order headlands, perennial, and woodland. Annual grasslands were too infrequently sampled to test, and mixed grasslands were not significantly localized ($p > 0.10$), although the modal frequency is closer to the coast (122 m) than that for the perennial type (244–488 m). More recent surveys suggest that succession toward greater dominance by perennial grasses is progressing. This analysis suggests that large scale vegetation unit patchiness is related to environmental gradients from the coastline inland.

We digitized the map and used the computer to estimate the area occupied by each vegetative unit. For the entire area of Sea Ranch, headlands cover approximately 3%, perennial grasslands 33%, mixed grasslands 11%, annual grasslands 2%, *Calamagrostis* 2%, woodland

47%, and 2% has no vegetation or is cultivated. For the coastal terrace only, headlands occupy 10%, perennial grasslands 38%, mixed grasslands 33%, annual grasslands 8%, *Calamagrostis* 5%, woodland 1%, and 5% has no vegetation or is cultivated.

The dominants of the 5 vegetation types sampled are given in Table 1. Dominance in this table is defined on the basis of frequency ($\geq$ 5% occurrence in all samples taken in a particular vegetation type) and relative cover ($\geq$ 5%; relative cover is defined as the summation of cover values of a species, normalized as a percentage of all cover values for all species). Despite this rather generous interpretation of dominance, no vegetation unit has more than 4 or less than 3 dominants even though the least rich type has 24 species. In each unit the small number of dominant species accounts for 62 to 92% of the total relative cover. Dominance is spread over a number of species, with only 3 (*Anthoxanthum odoratum*, *Holcus lanatus*, and *Rubus* spp.) dominant in more than one

TABLE 1. DOMINANT SPECIES OF FIVE VEGETATION TYPES AT SEA RANCH. Dominants have a frequency $\geq$ 5 samples and relative cover $\geq$ 5%. I = introduced species, N = native, A = annual, P = perennial, G = grass, F = forb, S = shrub or vine.

Vegetation type	Taxon	Life history pattern	Frequency (%)	Relative cover (%)
HEADLANDS	*Aira praecox*	IAG	100	34.87
	Hypochoeris radicata	NPF	100	26.47
	Lupinus variicolor	NPS	90	18.39
	Lasthenia chrysostoma	NAF	50	12.34
	Total			92.07
LUPINUS	*Lupinus arboreus*	NPS	96	28.27
	Anthoxanthum odoratum	IPG	63	16.90
	Holcus lanatus	IPG	86	16.33
	Total			61.50
MIXED	*Plantago lanceolata*	NPF	68	23.71
	Cynosurus echinatus	IAG	76	15.27
	Anthoxanthum odoratum	IPG	50	13.24
	Danthonia pilosa	IPG	69	11.64
	Total			63.86
PERENNIAL	*Deschampsia holciformis*	NPG	65	28.21
	Anthoxanthum odoratum	IPG	63	26.88
	Holcus lanatus	IPG	61	13.17
	Rubus spp.	NPS	36	5.11
	Total			73.37
CALAMAGROSTIS	*Calamagrostis nutkaensis*	NPG	100	55.15
	Rubus spp.	NPS	100	11.03
	Veratrum fimbriata	NPF	72	10.41
	Total			76.59

vegetation type. Among the dominants, perennials are predominant over annuals ($t = 4.01$, $p < 0.005$), with dominance among grasses, forbs, and shrubs differing from unit to unit ($F = 5.11$, $p < 0.025$). Annual forbs and grasses, perennial forbs, and prostrate shrubs (primarily *Lupinus variicolor*) are more important near the ocean than inland, where perennial grasses dominate to the near exclusion of everything else.

There is no significant difference in representation between native and introduced dominants ($t = 0.476$, $p > 0.50$).

Tables 2–6 present a quantitative list of all species in each of the vegetation types. For each taxon, we have tabulated the origin (introduced or native), the frequency of occurrence in samples, the percentage of relative cover, the mean absolute cover, and the standard error of mean absolute cover. A factor for converting relative cover to absolute cover is given in the legend for each table. Absolute cover is defined as the percentage of total sampled area actually covered by a species, and mean absolute cover is the sum of all cover values for that species divided by the number of plots in which it occurs.

By definition, the dominant species discussed above have high frequency and relative cover values, so it is expected that they have high mean cover values as well. However, there are many more species in each vegetation type of intermediate or low importance value. In Tables 2–6, these fall into 3 main groups: 1) species with high frequency and low cover values, i.e., species that are well dispersed; 2) species that are infrequent but which have high mean cover values; and 3) species that are both infrequent and low in cover value. The last category includes rare and unsuccessful species of little relative importance in the grassland, while the second is more complex because it includes infrequent but large species, and highly overdispersed species in the sense of Hairston (1959). *Myrica californica* is an example of the first, while *Cardionema ramosissimum, Juncus effusus* var. *brunneus,* and *Lasthenia chrysostoma* are examples of the second.

The patchiness observed between vegetation units (Fig. 1) may also be seen in the distribution of species among these units. Only 3 species (*Deschampsia holciformis, Hypochoeris radicata,* and *Horkelia californica*) were found in all 5 vegetation types, compared to 13 species in 4 of the 5 types, 20 in three, 30 in two, 26 in only one.

Within a type there is also considerable heterogeneity. The estimated standard errors, when converted into coefficients of variation, are lowest for dominants within each type. There are no evident trends, however, when nondominant species are considered. Some species are highly variable in mean cover (*Anagallis arvensis* is the best example); others are not (*Cynosurus echinatus* and *Danthonia pilosa,* Table 4). For those species occurring in more than one type, the coefficients of variation may differ widely (e.g., *Deschampsia holciformis,* Table 2, = 3.627; Table

5, = 0.169). Presumably the size of the coefficient is a function of colonization and species growth form as well as species interactions, but there is no clear trend.

Table 2. Cover Values of Species of the Sea Ranch Headlands Vegetation Type. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot, mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). Ten plots were sampled at one site. For conversion to absolute cover of each species multiply relative cover value by 0.79.

Taxon	I/N	F	RC	MC	SE
Annual Grasses					
Aira praecox	I	100	34.87	27.40	4.76
Bromus mollis	I	10	0.25	—	—
Festuca dertonensis	I	70	0.20	0.23	0.11
Bromus diandrus	I	10	t	—	—
Annual Forbs					
Lasthenia chrysostoma	N	50	12.34	19.40	5.22
Plantago hookeriana var. *californica*	N	40	0.20	0.39	0.11
Orthocarpus pusillus	N	30	0.06	0.34	0.17
Clarkia davyi	N	10	0.06	—	—
Daucus pusillus	N	10	0.01	—	—
Anagallis arvensis	I	10	t	—	—
Silene gallica	I	10	t	—	—
Biennial Grasses					
Bromus carinatus	N	20	0.01	0.05	0.00
Biennial Forbs					
Gnaphalium purpureum	N	10	0.95	—	—
Perennial Grasses					
Deschampsia holciformis	N	90	0.77	0.68	0.78
Hordeum californicum	N	90	0.65	0.57	0.19
Perennial Forbs					
Hypochoeris radicata	I	100	26.47	20.80	3.13
Plantago lanceolata	I	30	1.02	2.68	2.41
Convolvulus occidentalis var. *saxicola*	N	30	0.57	1.50	0.50
Cirsium quercetorum	N	10	0.25	—	—
Eschscholzia californica	N	10	0.25	—	—
Horkelia californica	N	10	0.06	—	—
Oxalis corniculata	I	20	0.07	0.32	0.19
Woody Vines, Shrubs, and Small Trees					
Lupinus variicolor	N	90	18.39	16.06	4.56
Longevity unknown					
Trifolium sp.	—	10	t	—	—
Bare Ground	—	—	2.44	—	—

TABLE 3. COVER VALUE OF SPECIES OF THE SEA RANCH LUPINE VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot, mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). 71 plots were sampled at one site. For conversion to absolute cover of each species multiply relative cover value by 1.10.

Taxon	I/N	F	RC	MC	SE
ANNUAL GRASSES					
Bromus diandrus	I	14.1	1.35	10.57	9.44
Bromus mollis	I	14.1	0.62	4.86	4.14
Aira caryophyllea	I	15.4	0.35	2.50	1.47
Gastridium ventricosum	I	1.4	0.20	—	—
Festuca dertonensis	I	15.4	0.13	0.93	0.71
Lagurus ovatus	I	4.2	0.03	0.08	0.06
Cynosurus echinatus	I	8.5	0.03	0.17	0.11
Hordeum leporinum	I	2.8	0.01	0.03	0.21
Briza minor	I	1.4	t	—	—
Lolium multiflorum	I	1.4	t	—	—
ANNUAL SEDGES AND RUSHES					
Juncus bufonius	N	2.8	0.12	4.75	2.75
ANNUAL FORBS					
Lotus angustissimus	I	7.0	3.02	47.30	17.37
Carduus pycnocephalus	I	1.4	0.10	—	—
Madia capitata	N	7.0	0.15	2.31	3.06
Geranium dissectum	I	2.8	t	0.10	0.00
Silene gallica	I	2.8	t	0.01	0.00
Lotus micranthus	N	1.4	t	—	—
ANNUAL OR BIENNIAL FORBS					
Cirsium brevistylum	N	1.4	0.10	—	—
Cirsium vulgare	I	4.2	0.20	5.20	5.15
PERENNIAL GRASSES					
Anthoxanthum odoratum	I	63.4	16.90	29.45	4.92
Holcus lanatus	I	85.9	16.33	21.00	3.38
Deschampsia holciformis	N	18.3	0.33	2.01	0.88
Lolium perenne	I	7.0	0.03	0.40	0.40
Danthonia pilosa	I	2.8	t	0.03	0.21
Elymus glaucus	N	1.4	t	—	—
PERENNIAL SEDGES AND RUSHES					
Juncus effusus var. *brunneus*	N	7.0	2.21	47.21	14.85
Cyperus eragrostis	N	1.4	0.62	—	—
Juncus effusus var. *pacificus*	N	3.9	0.42	5.33	1.29
Carex obnupta	N	1.4	0.20	—	—
Carex spp.	—	2.8	0.03	1.00	1.00
PERENNIAL FORBS					
Plantago lanceolata	I	15.5	0.94	6.68	2.20
Rumex acetosella	I	14.1	0.82	6.40	2.48
Horkelia californica	N	1.4	0.80	—	—
Hypochoeris radicata	I	19.7	0.61	3.40	1.30
Oenanthe sarmentosa	N	2.8	0.54	12.25	5.75
Cardionema ramosissimum	N	2.8	0.20	7.78	7.73
Stachys rigida	N	1.4	0.10	—	—

TABLE 3 (CONT.)

Taxon	I/N	F	RC	MC	SE
Abronia latifolia	N	1.4	0.10	—	—
Lotus corniculatus	I	2.8	0.03	2.00	0.00
Rumex sp.	—	1.4	t	—	—
Lythrum hyssopifolia	N	2.8	t	32.71	22.60
Mimulus guttatus	N	1.4	t	—	—
Veronica scutellata	N	1.4	t	—	—
WOODY VINES, SHRUBS, AND SMALL TREES					
Lupinus arboreus	N	95.8	28.37	32.72	3.87
Rubus ursinus—R. vitifolius	N	9.9	2.13	23.86	7.67
Salix spp.	N	2.8	0.22	8.75	6.75
FERNS					
Pteridium aquilinum var. *pubescens*	N	2.8	0.83	32.50	30.50
LONGEVITY UNKNOWN					
Galium spp.	—	2.8	0.20	7.75	7.75
Trifolium sp.	—	1.4	0.26	—	—
Lotus spp.	—	1.4	t	—	—
BARE GROUND		—	21.48	—	—

Species cover also varies depending on the time of year. Sampling was conducted in August and September when annuals had already dropped seed. Had an earlier sample been taken, comparison would probably show an increase in cover values for the annual species. A number of perennial species such as *Brodiaea laxa, Calochortus tolmiei* and *Ranunculus californicus* had been observed in the study sites during the spring but by August were not evident. The extent of cover increase of these species given an earlier sampling date is unknown, but we believe that their cover importance relative to all other species would remain minimal. Even at peak activity, these species are not dominants in the vegetation and therefore might be expected to change relative covers by no more than 5–10% at most.

Finally, the tables do not adequately reflect the small scale patchiness in each vegetation type. Within the perennial type, for example, some areas are almost exclusively *Deschampsia,* while in others *Holcus* is dominant, and in others, *Anthoxanthum* and *Danthonia pilosa.* Furthermore, there appears to be variation in patch size, from several hundred m^2 to less than one, with and without clear boundaries. By combining samples we have constructed an overall view of species composition in the grassland.

TABLE 4. COVER VALUES OF SPECIES OF THE SEA RANCH MIXED GRASSLAND VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot mean actual cover and standard error are not applicable and therefore indicated by a dash (—). 144 plots were sampled from four sites. For conversion to absolute cover of each species multiply relative cover value by 0.78.

Taxon	I/N	F	RC	MC	SE
ANNUAL GRASSES					
Cynosurus echinatus	I	75.7	15.27	15.74	1.96
Aira caryophyllea	I	67.4	3.45	3.99	0.73
Aira praecox	I	4.2	0.55	10.25	3.91
Bromus mollis	I	62.5	1.48	1.85	0.63
Festuca dertonensis	I	37.5	0.29	0.60	0.20
Briza minor	I	52.1	0.27	0.40	0.14
Lagurus ovatus	I	1.4	0.26	14.50	12.50
Bromus diandrus	I	12.5	0.24	1.39	0.81
Avena barbata	I	4.2	0.16	2.92	2.54
Hordeum leporinum	I	0.7	0.02	—	—
ANNUAL SEDGES AND RUSHES					
Juncus bufonius	N	1.4	0.02	1.25	0.75
ANNUAL FORBS					
Lasthenia chrysostoma	N	1.4	0.24	13.50	13.50
Lotus angustissimus	I	0.7	0.24	—	—
Sherardia arvensis	I	20.1	0.15	0.60	0.27
Hemizonia multicaulis	N	2.1	0.14	5.17	8.95
Silene gallica	I	26.4	0.12	0.35	0.20
Clarkia davyi	N	1.4	0.07	3.75	5.30
Anagallis arvensis	I	31.3	0.05	0.13	0.34
Geranium dissectum	I	2.8	0.02	0.50	0.50
Pogogyne serpylloides	N	0.7	0.02	—	—
Trifolium tridentatum	N	0.7	0.02	—	—
Plantago hookeriana var. *californica*	N	2.1	t	0.02	0.02
Madia capitata	N	1.4	t	0.01	0.00
Navarretia squarrosa	N	0.7	t	—	—
Trifolium dubium	I	0.7	t	—	—
Vicia benghalensis	I	0.7	t	—	—
BIENNIAL GRASSES					
Bromus carinatus	N	13.2	0.23	1.37	0.63
ANNUAL OR BIENNIAL FORBS					
Linum bienne	I	47.2	0.48	0.79	0.34
PERENNIAL GRASSES					
Anthoxanthum odoratum	N	50.7	13.24	20.37	2.70
Danthonia pilosa	I	69.4	11.64	13.08	1.99
Holcus lanatus	I	20.1	0.95	3.73	1.53
Stipa pulchra	N	22.9	0.40	1.38	0.42
Elymus glaucus	N	31.3	0.25	0.65	0.19
Deschampsia holciformis	N	7.6	0.13	1.37	0.66
Hordeum californicum	N	4.2	0.08	1.42	1.22
Lolium perenne	I	19.4	0.04	0.16	0.08
Danthonia californica	N	0.7	t	—	—

Table 4 (Cont.)

Taxon	I/N	F	RC	MC	SE
Perennial Sedges and Rushes					
Juncus effusus var. *brunneus*	N	2.1	0.31	11.50	8.05
Juncus effusus var. *pacificus*	N	0.7	0.07	—	—
Carex spp.	N	0.7	t	—	—
Eleochoeris palustris	N	0.7	t	—	—
Perennial Forbs					
Plantago lanceolata	I	68.5	23.71	21.48	1.57
Iris douglasiana	N	9.7	3.74	20.04	5.61
Hypochoeris radicata	I	34.7	1.24	2.79	0.65
Horkelia californica	N	7.6	1.01	11.31	2.65
Corethyrogyne californica var. *obovata*	N	2.8	0.66	—	—
Achillea borealis ssp. *arenicola*	N	5.6	0.58	8.19	4.99
Convolvulus occidentalis var. *saxicola*	N	7.6	0.52	5.33	1.77
Cardionema ramosissimum	N	1.4	0.39	22.00	2.00
Rumex acetosella	I	17.4	0.31	1.42	0.55
Stachys rigida	N	1.4	0.14	8.00	7.50
Aster chiloensis	N	1.4	0.08	4.75	3.89
Plantago hirtella var. *galeottiana*	N	0.7	0.07	—	—
Fragaria chiloensis	N	1.4	0.02	1.03	0.98
Oxalis corniculata	I	1.4	0.02	1.00	1.00
Sisyrinchium bellum	N	1.4	t	0.05	0.00
Lythrum hyssopifolia	N	2.1	t	0.02	0.02
Brodiaea coronaria	N	1.4	t	0.03	0.02
Epilobium watsonii var. *franciscanum*	N	0.7	t	—	—
Veronica scutellata	N	0.7	t	—	—
Woody Vines, Shrubs, and Small Trees					
Rubus ursinus—R. vitifolius	N	27.8	4.67	13.13	1.56
Salix lasiolepis	N	0.7	0.85	—	—
Lupinus arboreus	N	2.1	0.04	1.50	0.50
Ferns					
Pteridum aquilinum var. *pubescens*	N	10.4	1.56	11.70	2.47
Longevity Unknown—Forbs					
Trifolium spp.	—	1.4	t	0.03	0.02
Lotus spp.	—	2.1	t	0.01	0.00
Galium spp.	—	0.7	t	—	—
Bare Ground			10.13		

TABLE 5. COVER VALUES OF SPECIES OF THE SEA RANCH PERENNIAL GRASSLAND VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species occurs in only one plot mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). 181 plots were sampled from 3 sites. For conversion to absolute cover of each species multiply relative cover value by 0.96.

Taxon	I/N	F	RC	MC	SE
ANNUAL GRASSES					
Aira caryophyllea	I	33.7	1.24	3.55	1.03
Bromus mollis	I	28.2	0.83	3.60	1.34
Aira praecox	I	7.2	0.39	5.27	2.36
Lagurus ovatus	I	6.6	0.31	4.50	3.46
Festuca dertonensis	I	22.1	0.29	1.30	0.55
Briza minor	I	23.2	0.12	5.19	0.52
Cynosurus echinatus	I	12.2	0.06	0.50	0.17
Avena barbata	I	1.7	0.01	0.84	0.09
Bromus diandrus	I	3.3	t	0.01	0.00
ANNUAL SEDGES AND RUSHES					
Juncus bufonius	N	0.5	t	—	—
ANNUAL FORBS					
Sherardia arvensis	I	4.4	0.02	0.30	0.11
Trifolium dubium	I	1.7	0.01	0.80	0.58
Silene gallica	I	7.2	t	0.10	0.03
Plantago hookeriana var. *californica*	N	1.7	t	0.20	0.17
Anagallis arvensis	I	5.0	t	0.06	0.06
Pogogyne serpylloides	N	0.5	t	—	—
Hemizonia multicaulis	N	1.1	t	—	—
Lotus angustissimus	I	1.1	t	0.01	0.00
Galium aparine	I	1.1	t	0.03	0.02
Geranium dissectum	I	3.3	t	0.10	0.08
Orthocarpus castillejoides	N	1.1	t	0.03	0.02
Daucus pusillus	N	1.1	t	0.01	0.00
Clarkia davyi	N	0.5	t	—	—
Lotus micranthus	N	1.1	t	0.01	0.00
Madia capitata	N	1.4	t	0.01	0.00
Trifolium spp.	—	0.5	t	—	—
Vicia benghalensis	I	0.5	t	—	—
BIENNIAL GRASSES					
Bromus carinatus	N	1.7	t	0.17	0.17
BIENNIAL FORBS					
Erechtites prenanthoides	I	1.1	0.09	7.80	7.85
Gnaphalium purpureum	N	3.3	0.01	0.18	0.07
Erechtites arguta	I	0.5	t	—	—
ANNUAL OR BIENNIAL FORBS					
Linum bienne	I	10.5	0.01	0.33	0.12
PERENNIAL GRASSES					
Deschampsia holciformis	N	65.2	28.21	41.61	2.22
Anthoxanthum odoratum	I	63.0	26.91	32.48	2.48

TABLE 5 (CONT.)

Taxon	I/N	F	RC	MC	SE
PERENNIAL GRASSES (continued)					
Holcus lanatus	I	61.3	13.18	20.65	2.43
Calamagrostis nutkaensis	N	0.5	0.55	—	—
Hordeum californicum	N	7.7	0.09	4.00	2.00
Danthonia pilosa	I	12.2	0.07	0.58	0.35
Elymus glaucus	N	5.5	t	0.10	0.01
Danthonia californica	N	2.8	t	0.14	0.01
Lolium perenne	I	2.2	t	0.01	0.00
Festuca arundinacea	I	0.5	t	—	—
PERENNIAL SEDGES AND RUSHES					
Juncus effusus var. *brunneus*	N	6.6	1.59	15.34	9.16
Carex spp.	N	7.2	0.48	6.39	2.34
Carex obnupta	N	2.2	0.29	12.63	5.69
Juncus effusus var. *pacificus*	N	6.1	0.10	1.51	0.66
PERENNIAL FORBS					
Plantago lanceolata	I	50.2	4.92	10.51	1.05
Hypochoeris radicata	I	37.0	1.89	5.86	0.94
Iris douglasiana	N	20.4	1.59	7.47	1.28
Rumex acetosella	I	14.4	0.28	1.85	0.72
Fragaria chiloensis	N	4.4	0.24	5.13	2.43
Aster chilensis	N	0.5	0.09	—	—
Cirsium quercetorum	N	0.5	0.09	—	—
Eryngium armatum	N	3.9	0.08	1.86	0.98
Acaena californica	N	0.5	0.04	—	—
Oxalis corniculata	I	2.8	0.01	0.42	0.39
Sisyrinchium bellum	N	1.7	0.01	0.35	0.15
Convolvulus occidentalis var. *saxicola*	N	1.1	t	0.28	0.02
Horkelia californica	N	1.1	t	0.28	0.02
Lotus corniculatus	I	1.1	t	0.01	0.00
Cardionema ramosissimum	N	0.5	t	—	—
Scrophularia californica	N	0.5	t	—	—
WOODY VINES, SHRUBS, AND SMALL TREES					
Rubus ursinus—R. vitifolius	N	35.9	5.11	13.68	1.85
Lupinus arboreus	N	15.5	2.15	13.36	2.55
Myrica californica	N	0.5	0.55	—	—
Lupinus variicolor	N	1.1	0.02	2.00	0.00
FERNS					
Pteridium aquilinum var. *pubescens*	N	19.9	2.48	11.98	2.24
UNKNOWN LONGEVITY—FORBS					
Galium spp.	—	0.5	0.09	—	—
Lotus spp.	—	1.1	t	0.01	0.00
BARE GROUND		—	5.93	—	—

TABLE 6. COVER VALUE OF SPECIES OF THE SEA RANCH CALAMAGROSTIS VEGETATION TYPE. I/N = introduced (I) or native (N); F = frequency of occurrence (percent of total samples); RC = percent relative cover; MC = mean actual percent cover; SE = standard error of mean actual percent cover; t = species present, relative cover < 0.01%. When a species only occurs in one plot mean actual percent cover and standard error are not applicable and therefore indicated by a dash (—). 25 plots were sampled at one site. For conversion to absolute cover of each species multiply relative cover value by 1.10.

Taxon	I/N	F	RC	MC	SE
ANNUAL FORBS					
Sonchus asper	I	8	t	0.03	3.33
BIENNIAL FORBS					
Erechtites prenanthoides	I	36	2.21	6.73	3.07
Erechtites arguta	I	8	0.02	0.28	0.23
ANNUAL OR BIENNIAL FORBS					
Cirsium vulgare	I	4	t	—	—
PERENNIAL GRASSES					
Calamagrostis nutkaensis	N	100	55.15	61.50	3.83
Elymus glaucus	N	24	3.49	15.94	15.91
Holcus lanatus	I	100	3.14	3.49	0.88
Anthoxanthum odoratum	I	28	0.08	0.32	0.29
Deschampsia holciformis	N	20	t	0.03	0.01
PERENNIAL SEDGES AND RUSHES					
Carex obnupta	N	60	5.77	10.54	3.06
Juncus effusus var. *brunneus*	N	52	0.48	1.01	0.58
Carex spp.	N	8	t	0.01	0.00
Juncus effusus var. *pacificus*	N	4	t	—	—
PERENNIAL FORBS					
Veratrum fimbriata	N	72	10.41	16.88	1.59
Oenanthe sarmentosa	N	60	2.18	3.97	0.78
Iris douglasiana	N	68	2.13	3.42	1.23
Vicia gigantea	N	64	0.74	1.27	0.47
Galium trifidum var. *subbiflorum*	N	48	0.63	1.44	0.83
Stachys rigida	N	48	0.51	1.18	0.61
Veronica scutellata	N	52	0.34	0.71	0.23
Mimulus moschatus	N	32	0.29	1.01	0.30
Campanula californica	N	64	0.23	0.39	0.17
Sidalcea malvaeflora	N	4	0.07	—	—
Achillea borealis ssp. *arenicola*	N	4	t	—	—
Horkelia californica	N	4	t	—	—
Hypochoeris radicata	I	4	t	—	—
Smilacina stellata var. *sessilifolia*	N	4	t	—	—
WOODY VINES, SHRUBS, AND SMALL TREES					
Rubus ursinus—R. vitifolius	N	100	11.03	12.16	1.79
Myrica californica	N	4	0.27	—	—

TABLE 6 (CONT.)

Taxon	I/N	F	RC	MC	SE
FERNS					
Pteridium aquilinum var. *pubescens*	N	8	0.28	3.78	3.73
LONGEVITY UNKNOWN					
Trifolium spp.	—	4	t	—	—
BARE GROUND		—	0.46	—	—

DISCUSSION

Floristic comparisons between the Sea Ranch grasslands and other areas of coastal prairie show a consistent set of characteristic species. In a 1902 description of the north coast prairie, Davy stated that the prevailing grasses were *Danthonia californica, Festuca rubra, Calamagrostis aleutica* (now *C. nutkaensis*), and *Deschampsia caespitosa.* These native perennial grasses have now been joined by a number of introduced grasses that are an equally important component of today's grasslands: *Holcus lanatus, Anthoxanthum odoratum, Agrostis tenuis, Festuca arundinacea,* and *Danthonia pilosa* (Beetle, 1947; Peñalosa, 1963; Howell, 1970; Batzli and Pitelka, 1970; Crampton, 1974; Elliott and Wehausen, 1974; Heady et al., 1977).

Some of the non-grass species also considered to be indicators of the coastal prairie are *Iris douglasiana, Carex tumicola, Carex obnupta, Camassia quamash* var. *linearis, Spiranthes romanzoffiana, Viola adunca,* and *Juncus effusus.* Most of these are more or less restricted to the coastal area, but various floral descriptions include an even greater number of species that are also common to the annual grasslands inland. Some of the more prominent species include *Aira caryophyllea, Briza minor, Avena barbata, Avena fatua, Bromus mollis, Bromus diandrus, Lolium multiflorum, Brodiaea pulchella, Sisyrinchium bellum, Lasthenia chrysostoma, Eschscholzia californica,* and *Plantago lanceolata.*

Note that most of these species were found at Sea Ranch. However, the data emphasize patchiness over uniformity: patchiness in the distribution of vegetation units, patchiness of species and dominant distributions from area to area, and patchiness within any one area. Clearly, the Sea Ranch grasslands are not uniform entities and part of the patchiness must result from variation in the physical environment. For example, Barbour et al. (1973) have shown that soil salinity decreases inland. At Bodega Head they showed that the higher salinity near the bluffs and the physical effects of onshore winds affect the distribution of certain species (*Lupinus arboreus,* in particular). In drier areas *Festuca idahoensis* and *Danthonia californica* may be more important dominants than

Deschampsia holciformis or *Calamagrostis nutkaensis* (Huffaker and Kennett, 1959; Crampton, 1974). Other than the restriction of the headlands type to exposed bluffs and the *Calamagrostis* type to very wet-claypan areas, we have not observed obvious correlations between presumed soil gradients and grassland vegetation type. In particular, the distributions of major soil types (U.S.D.A., 1972) and vegetation types seem unrelated, although Baywood soils do tend to be immediately adjacent to the ocean bluffs and the Rohnerville soils further inland.

Soil moisture is probably a factor in the distribution of at least some species. Since the area is made up of a series of terraces, the inland soils are older and deeper, and this, together with the fact that the ridge behind the terrace receives twice the amount of rainfall, suggests that the terrace areas at the base of slopes receiving the greatest amount of runoff might be particularly favorable for perennial development. The southern portion of Sea Ranch, with its narrow terrace, apparently permits enough seepage and runoff to support the stands of *Calamagrostis* there. In this case, the *Calamagrostis* vegetation type indicates the abundance of water.

In addition to the effects of physical environment, we feel that disturbance (grazing and construction) has a large influence on species composition. This finds some support in the literature. Burcham (1957) suggests that perennials disappeared from California's Central Valley under grazing pressures. Similarly, Clements and Shelford (1939) stated that three-fourths of the land south of Mt. Shasta, and from the coast to the foothills of the Sierra Nevada in Northern California, was originally perennial climax grassland and that replacement by annuals was largely caused by overgrazing. Hormay and Fausett (1942) estimated that 90–100% of the forage available on heavily grazed rangeland consisted of annuals. With perennials remaining green throughout the dry summer season, they are subject to heavy use, which reduces plant vigor and leaves space for the increase of less palatable species characteristic of earlier seral stages (Burcham, 1957).

Huffaker and Kennett (1959) documented an example in Humboldt County where prior range practices had changed a once-perennial grassland dominated by *Danthonia californica* to one of mostly annuals. By withholding grazing until seed shattered and by rotating grazing, perennials again increased. More recently, Elliott and Wehausen (1974) showed that the coastal grassland at Pt. Reyes was highly responsive to grazing. With increased grazing pressure, there was an increase of exotic annual species and a decrease in the native, predominantly perennial vegetation. In particular, perennial species dominant at the Sea Ranch were prominent when protected from grazing at Pt. Reyes (*Deschampsia holciformis*, e.g.).

With grazing having ended less than 10 years earlier, we have shown that the grassland at the Sea Ranch is dominated by perennials, although no one species has yet established anything approaching uniform dominance. This analysis enables us to make some predictions to be confirmed by future sampling of the vegetation: we expect the dominant perennial grasses to continue to spread and increase their cover values, and to this extent to clarify the picture of succession within the grassland from annuals to perennials. We expect the restricted areas of annual grasses to become more scarce and more restricted to areas of disturbance, and the mixed grasslands to become perennial grasslands within a few years.

Acknowledgments

Support was provided by grants to the Division of Environmental Studies, U.C. Davis, from the Rockefeller Foundation, from the University of California Council for Advanced Studies of the Environment, and from the North Coast Institute. We thank Cathy Hendel Bowen for her invaluable field assistance, and B. Crampton and J. McCaskill for aid in species identification. We are grateful to the U.S. Army Corps of Engineers, especially Mr. Michael Murphy, for use of their NASA aerial photographs. Special thanks go to the members of the Sea Ranch Association, particularly G. Wickstead, W. Crooks, R. Kirkwood, C. Kuhn, J. Wingate, and I. Morgan, as well as the North Coast Institute, for providing the research site and general support. We are indebted to S. K. Jain, J. Major, and G. Webster, for helpful criticism of an earlier draft of this manuscript.

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